

COMPARATIVE MORPHOLOGY OF THE SEXUALLY DIMORPHIC ORB-WEAVING SPIDER *ARGIOPE BRUENNICHI* (ARANEAE: ARANEIDAE)

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Müller, M.C. and Westheide, W. 1993 11 11: Comparative morphology of the sexually dimorphic orb-weaving spider *Argiope bruennichi* (Araneae: Araneidae). *Memoirs of the Queensland Museum* 33(2): 615-620. Brisbane. ISSN 0079-8835.

Although the web building spigots of the glandulae aggregatae and the glandulae flagelliformes are not functional in mature males, adult *Argiope bruennichi* and *A. lobata* males are able to build webs. The structure of these webs is described. The aciniform spigots on the intermediate spinnerets of *A. bruennichi* males have degenerated to a great extent. Culture experiments with *A. bruennichi* enabled us to follow differences in the development of female and male morphology. The presence of the tubuliform spigots in the sixth instar suggests one possible evolutionary hypothesis concerning sexual dimorphism in spiders.

Nach der Reifehäutung sind die aggregaten und flagelliformen Spulen—welche als Triade die Fangfäden sezernieren—auf den hinteren Spinnwarzen der Männchen nur rudimentär ausgebildet. Trotz dieser Reduktion spannen adulte *Argiope bruennichi* und *A. lobata* Männchen Radnetze, deren Struktur beschrieben wird. Auf den mittleren Spinnwarzen subadulter und adulter *A. bruennichi* Männchen ist ein hoher Prozentsatz der aciniformen Spulen unvollständig ausgebildet. Durch Aufzucht der Wespenspinne war es möglich, morphologische geschlechtsspezifische Unterschiede in der Postembryonalentwicklung festzustellen. Das frühe Auftreten der tubuliformen Spulen im weiblichen Spinnapparat kann als Argument für eine Hypothese zur Evolution des Sexualdimorphismus interpretiert werden. □% *Development, sexual size dimorphism, spinning apparatus, male orb-webs, tubuliform spigot.*

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Sexual dimorphism varies across taxa, but the question of whether highly dimorphic species occur as a result of selection for large female or small male size remains controversial.

Gerhardt (1924) observed that both carnivorous feeding habits and cannibalism endanger male spiders before, during and after copulation (Elgar and Nash, 1988). Darwin (1890) and Bristowe (1929) suggested that their small size protects the males from the females which do not recognize males of reduced size as prey. In contrast, Gerhardt (1924) and Vollrath (1980) argue that 'the females have evolved to be larger, allowing greater egg production' (Vollrath, 1980: 165).

Morphological investigations of sexual size dimorphism are rare; for example Sekiguchi (1955a, b) compared the spinning apparatus in male and female spiders. The present investigation examines whether or not there are morphological data that could be used to assess these different ideas, by analysing the spinning apparatus in different instars of *Argiope bruennichi*.

MATERIALS AND METHODS

Adult males and females of *Argiope bruennichi*

(Scopoli, 1772) were collected from Dabas (Hungary), and subadult males and cocoons from Wittenberg-Lutherstadt (Germany).

Specimens of *A. bruennichi* were raised individually from the third instar. Some individuals from each instar were fixed in Carnoy's fluid immediately after moulting. The lengths and widths of the prosoma were measured. For SEM studies the spinning apparatus was removed and the spinnerets were dehydrated in ethanol and critical point dried with carbon dioxide. After sputtering with gold, they were analysed with a Cambridge Stereoscan 250. For light microscopy the spinnerets were separated into smaller pieces and embedded in Swann-fluid.

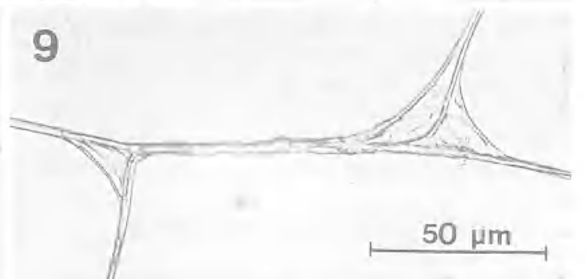
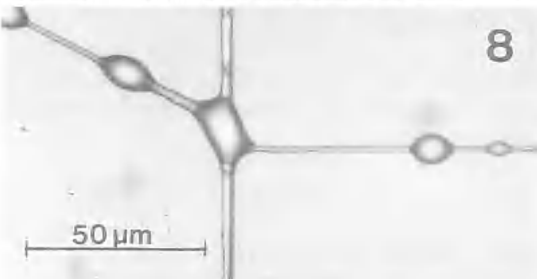
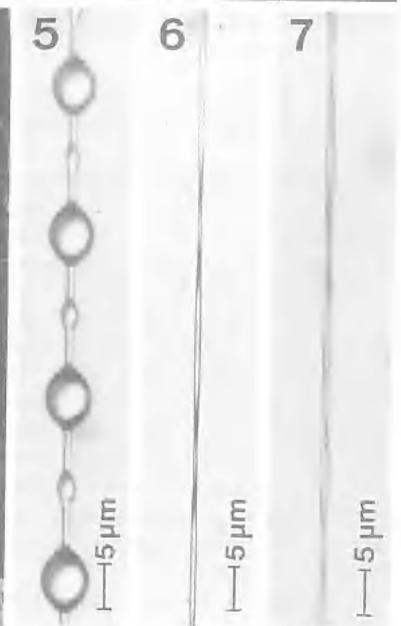
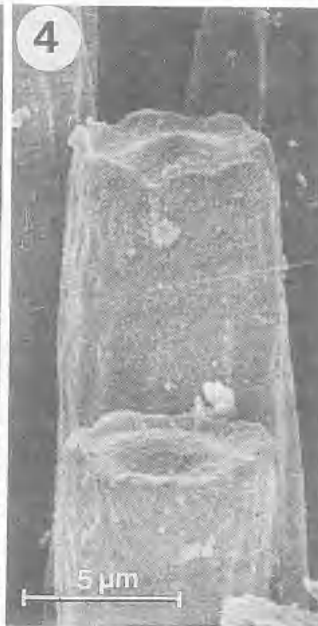
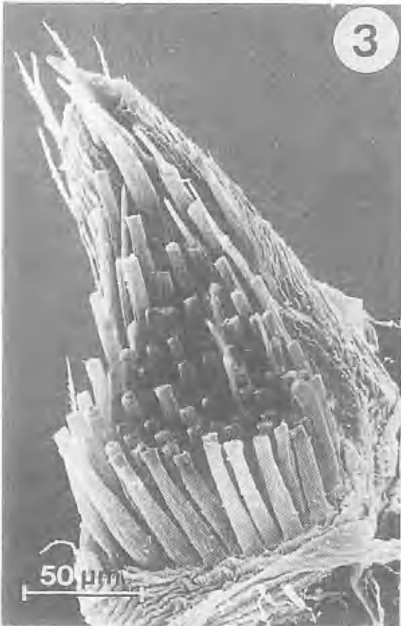
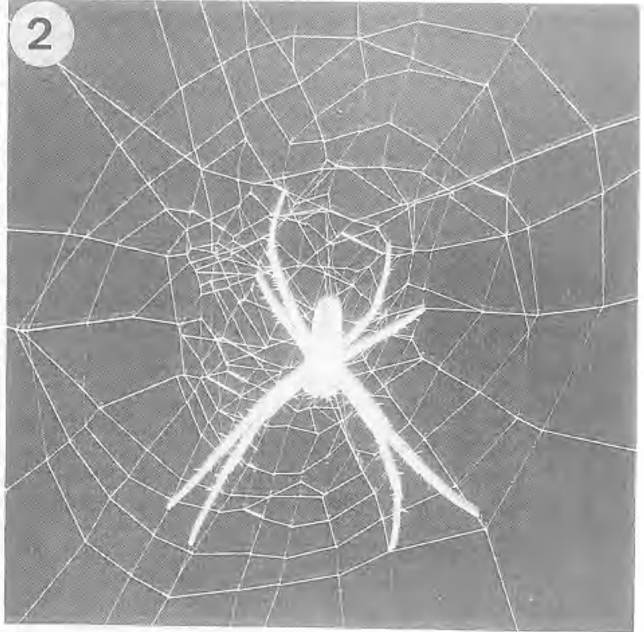
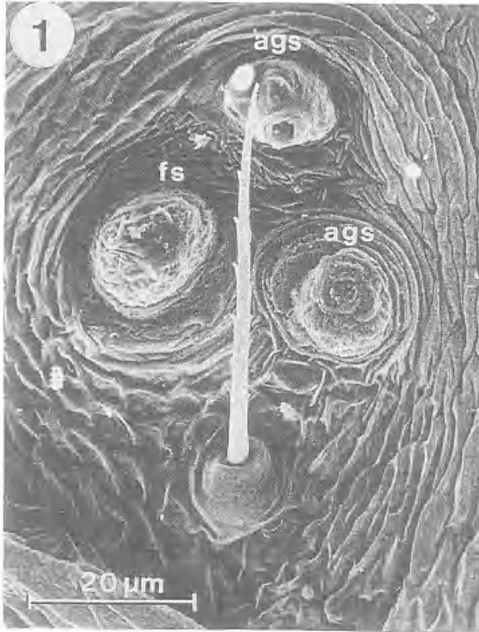
Subadult males of *A. bruennichi* were kept in plexiglass frames from the penultimate stadium until they died.

Early instars were fed with greenflies (Aphidina) and *Drosophila melanogaster* while older stages were provided with various insects captured in the field.

RESULTS

ADULT *ARGIOPE* MALES CAN SPIN WEBS

The posterior spinnerets of adult males are





equipped only with rudimentary projections of the triad spigots (Fig. 1). These aggregate and flagelliform spigots—which usually furnish the capture threads—obviously do not function. Nevertheless, adult males of *A. bruennichi* and *A. lobata* spun rudimentary orb-webs (Fig. 2). These webs were destroyed every day during our study and the spiders renewed them almost daily. Subadult males spun normal orb-webs with the typical stabilimentum until the last moult. Webs spun after the terminal moult were smaller than subadult webs. They showed an irregular structure; but radia and a spiral were present. This spiral consisted of a few turns with remarkably increasing space outwards thus showing a closer resemblance to the auxiliary spiral than to the capture spiral. No droplets adhered to the spiral threads when the spiders were sprayed with water using an atomiser. They seemed to be thinner than capture threads and were not sticky. Prey thrown into the webs did not adhere to the spiral threads. A microscopical investigation revealed that their structure also strongly resembled auxiliary threads (Figs 5-7). The auxiliary nature of the web was confirmed by comparing the connection points of different types of threads with the radia (Figs 8-9).

INTERMEDIATE SPINNERETS OF ADULT MALES

The number of piriform and aciniform spigots for each sex were counted under the light microscope. There were fewer bases than apical parts of the aciniform spigots in the intermediate spinnerets of males. SEM examinations showed that a surprisingly high number of apical parts were degenerated (Figs 3-4). Only 19.2% (6 individuals) of the aciniform spigots on the intermediate spinnerets were fully developed. This degeneration was less in subadult males.

POSTEMBRYONIC DEVELOPMENT OF BODY SIZE

The shape of the opisthosoma changed during the development of *A. bruennichi*. The spherical form changed into an elongated one, reaching the proportion of adult spiders at the sixth instar. This pattern is clearly shown by the length/width-quotient of the opisthosoma in each instar (see Table 1). The development of both prosoma and opisthosoma was nearly uniform for all individuals until the sixth instar, although the inter-

	II	III	IV	V	VI	VII	VIII	♂	♀
	1.3	1.4	1.4	1.6	1.9	1.8	2.0	1.9	1.9
S.D.	0.09	0.08	0.04	0.09	-	-	-	0.14	0.56

TABLE 1. *Argiope bruennichi*. Length/width-quotients and standard deviation of the opisthosoma for different instars (II-VIII) and adults (n = 62).

vals between the moults varied (instar III to IV: 17-73 days; instar IV to V: 11-52 days). Following the sixth instar (when subadult males could be first determined) the sexes developed differently (Fig. 15). This pattern of development of sexual dimorphism is less apparent in the prosoma.

POSTEMBRYONIC DEVELOPMENT OF THE SPINNING APPARATUS

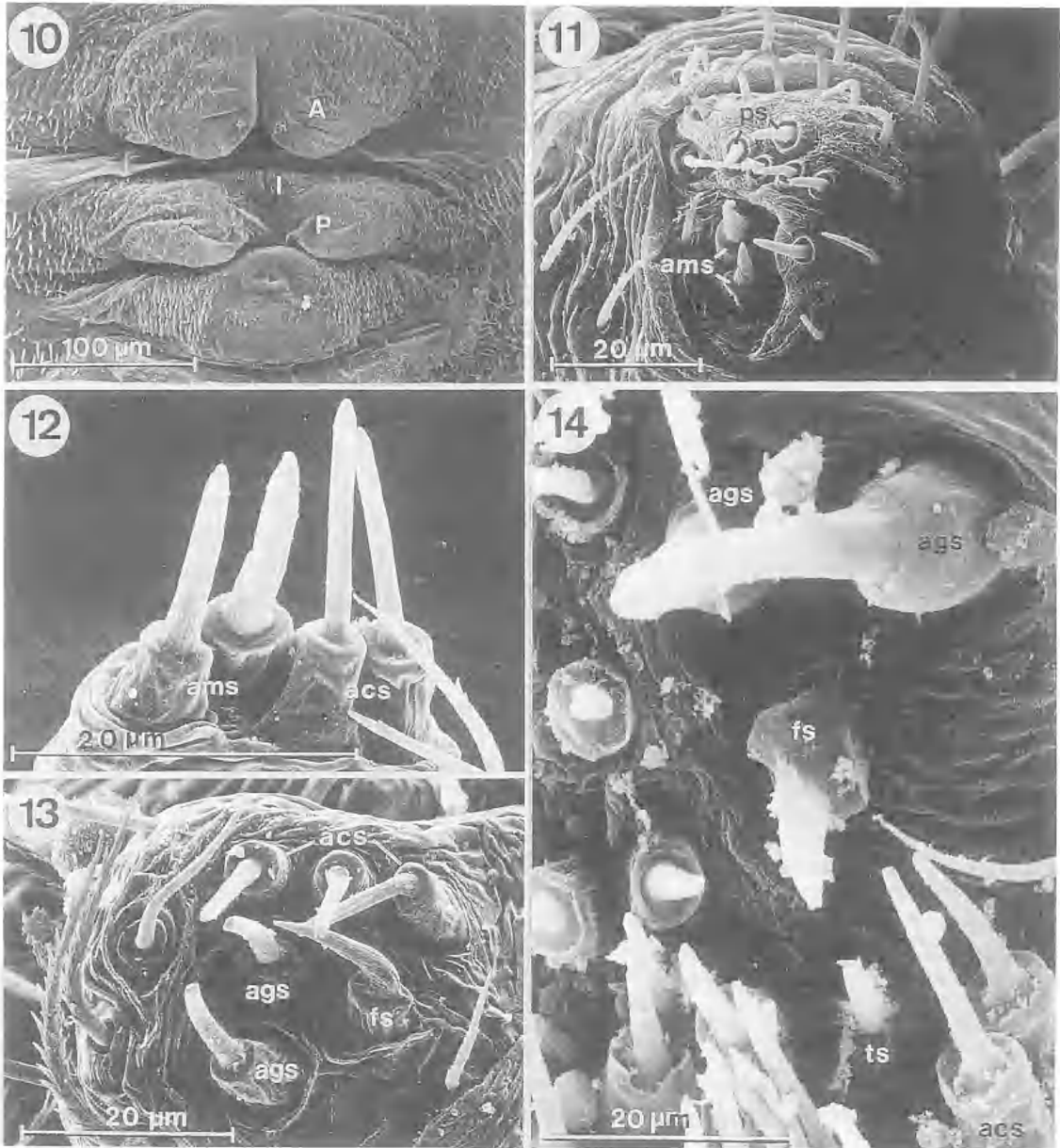
The development of the spinnerets was documented by counting the piriform and aciniform spigots. None of these fusules was found in the second instar (Fig. 10). Six piriform (anterior spinnerets), two aciniform (intermediate spinnerets) and three aciniform spigots (posterior spinnerets) were counted for third instar individuals (Figs 11-13). The development of the spigot number was uniform until the sixth instar. From that stadium on, the sexes developed differently as shown for the aciniform spigots on the posterior spinnerets (Fig. 16). Although the anterior and intermediate spinnerets develop in the same way (Fig. 16), the differentiation of the sexes is less obvious.

Tubuliform spigots were also first observed in the sixth instar of female spiderlings (Fig. 14).

DISCUSSION

The degeneration of the triad spigots on male posterior spinnerets during the terminal moult was first described by Sekiguchi (1955b) and subsequently documented for other species. These morphological reductions in males were explained by changes in their behaviour: adult males cease spinning webs and instead search for females. Emerton (1878) and McCook (1890) mentioned that small webs were spun by *Argiope aurantia* males, but no information about the structure of these webs was provided. This study shows that *A. bruennichi* and *A. lobata* males are capable of spinning webs. The spiral threads of

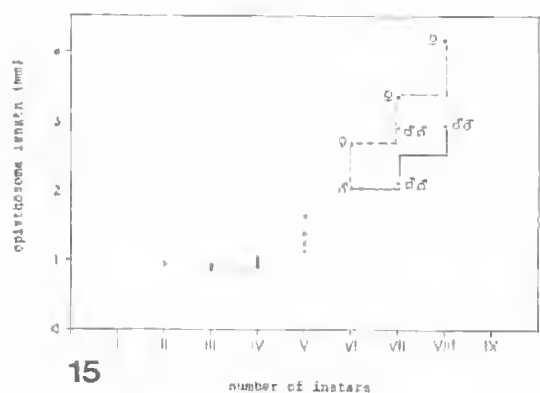
FIGS. 1-9. 1. Triad spigots at posterior spinneret of adult male. Apical parts of aggregate (ags) and flagelliform (fs) spigots missing, bases vestigial. 2. Orb-web of adult *Argiope bruennichi* male. 3. Intermediate spinneret of adult male. Many apical parts of aciniform spigots missing. 4. Detail of 3. 5-9. Different structures of male webs. 5: Capture thread (subadult male); 6: Auxilliary thread (subadult male); 7: Spiral thread (adult male); 8: Junction of a capture thread with a radia; 9: Junction of a spiral thread with a radia.



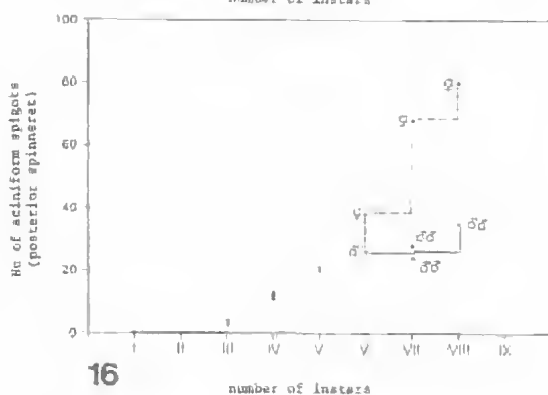
FIGS 10-14. Developmental stages of spinning apparatus. 10: Second instar; anterior (A), intermediate (I) and posterior spinnerets (P) are undeveloped; 11-13: Third instar; 11: Anterior spinneret with six piriform (ps) and two ampullate (ams) spigots; 12: Intermediate spinneret with two aciniform (acs) and two ampullate (ams) spigots; 13: Posterior spinneret with three aciniform spigots (acs) and the triad (consisting of two aggregate (ags) and one flagelliform (fs) spigots); 14: Detail of posterior spinneret of ♀ spiderling at sixth instar. Tubuliform spigot (ts) is clearly to differentiate from aciniform spigots (acs). Note arrangement of triad: aggregate (ags) and flagelliform (fs) spigots stay apart from each other, typical for subadults.

these webs resemble auxiliary threads, and therefore are not furnished by the triad glands which still exist immediately after the last moult (see Sekiguchi, 1955b). The auxiliary thread type was

recognized because the threads were not covered with glue droplets. However, it is possible that these threads are not auxiliaries: Vollrath and Edmonds (1989) found that the glue is soluble in



15



16

FIGS 15-16. Postembryonic development of *Argiope bruennichi*: 15: Opisthosoma length; 16: Number of aciniform spigots at posterior spinneret.

water and Peters and Kovoor (1991) argue that the glue does not necessarily fall into droplets.

It is not clear why adult males produce these rudimentary webs, but their poor design suggests that it is unlikely that they function to catch prey. That adult males rejected food offered with tweezers can support this assumption.

The females in spider genera that exhibit extreme size dimorphism are usually hemisessile. Thus courtship and mating is achieved by male mobility. Male mobility is achieved by using bridging lines and ballooning (Peters, 1990). McCook (1890) described these balloon lines as consisting of quite a number of threads that remain separated from one another, which suggests that they are furnished by the aciniform spigots. The degeneration of these aciniform spigots on the intermediate spinnerets of adult *Argiope bruennichi* males may occur because the remaining spigots are sufficient to produce the balloon lines. Alternatively, these threads may originate from other spigots. If the aciniform

spigots of the posterior spinnerets furnish the balloon lines, then their degeneration on the intermediate spinnerets would not disadvantage the males. Since adult males do not depend on the additional function of the aciniform threads (in terms of prey wrapping) their degeneration may be interpreted as a morphological adaptation to an altered style of life.

These results suggest that the development of sexual dimorphism takes place in the sixth instar.

Townley *et al.* (1991) reported tubuliform spigots in *Araneus cavaticus* in the fourth instar, which is equivalent to the sixth instar of *Argiope*. Townley *et al.* (1991) suggested that the tubuliform spigots are present that early in order to 'stake out sites for the functioning spigots of mature females, because the tubuliform glands are poorly developed and do not serve any function at that time'. This explanation seems unlikely because the spinnerets are reorganized and the number of fusules increases with each moult.

In contrast, we consider the existence of the tubuliform spigots already at the sixth instar in female spiderlings to be an indication for the hypothesis that phylogenetically earlier females reached maturity at this developmental stage.

In females the tubuliform spigots may indicate the penultimate stadium as do the swollen palpi in males. While the males become mature, females undergo another series of moults (3-4) to reach maturity. During their phylogenetic history, the females in the subadult stage—more exactly in the penultimate stadium—undergo a prolongation of their development resulting in a larger body size, directly correlated with higher egg production. Therefore, sexual size dimorphism may have evolved to produce larger females, a hypothesis as especially presented by Gerhardt (1924) and Vollrath (1980).

ACKNOWLEDGEMENTS

We wish to thank Dr. Peter Sacher (Wittenberg-Lutherstadt, Germany) for valuable discussions and for the *Argiope* material.

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